

Copepod community structure and abundance in a tropical mangrove estuary, with comparisons to coastal waters

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Published online: 4 February 2010
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Abstract Zooplankton, sampled at five stations from the upper Sangga estuary (7 km upstream) in Matang Mangrove Forest Reserve (MMFR), Malaysia, to 16 km offshore, comprised more than 47% copepod. Copepod abundance was highest at near-shore waters (20,311 ind m⁻³), but decreased toward both upstream (15,572 ind m⁻³) and offshore waters (12,330 ind m⁻³). Copepod abundance was also higher during the wetter NE monsoon period as compared to the drier SW monsoon period, but vice versa for copepod species diversity. Redundancy analysis (RDA) shows that copepod community structure in the upper estuary, nearshore and offshore waters differed, being influenced by spatial and seasonal variations in environmental conditions. The copepods could generally be grouped into estuarine species (dominantly *Acartia spinicauda* Mori, *Acartia* sp1, *Oithona aruensis* Früchtl, and *Oithona dissimilis* Lindberg), stenohaline species (*Acartia erythraea* Giesbrecht, *Acrocalanus gibber* Giesbrecht, *Paracalanus aculateus* Giesbrecht, and *Corycaeus andrewsi* Farran) and euryhaline species (*Parvocalanus crassirostris* Dahl, *Oithona simplex*

Farran, and *Bestiolina similis* (Sewell)). Shifts in copepod community structure due to monsoonal effects on water parameters occurred at the lower estuary. Copepod peak abundance in mangrove waters could be associated with the peak chlorophyll *a* concentration prior to it. Evidence of copepod consumption by many species of young fish and shrimp larvae in the MMFR estuary implies the considerable impact of phytoplankton and micro-phytobenthos on mangrove trophodynamics.

Keywords Community structure · Abundance · Copepods · Mangrove estuary · Coastal waters

Introduction

The mangrove habitat has been regarded as a zooplankton-rich area (Robertson & Blaber, 1992) serving as feeding and nursery ground for a variety of fishes and invertebrates (Robertson & Duke, 1987; Sasekumar et al., 1994; Laegdsgaard & Johnson, 2001; Chong, 2007). The high productivity of the mangrove ecosystem has always been linked to its largely detritus-based food web with mangrove supplying the main source of carbon to aquatic consumers (Lugo & Snedaker, 1974; Odum & Heald, 1975). However, this role of mangrove has recently been questioned and debated (e.g., Loneragan et al., 1997; Chong et al., 2001; Bouillon et al., 2003; Lee,

Guest editors: L. Sanoamuang & J. S. Hwang / Copepoda: Biology and Ecology

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2005) with the advent of stable isotope (DeNiro & Epstein, 1978; Peterson & Fry, 1987) and fatty acid tracers (Meziane & Tsuchiya, 2000, 2002) techniques. Arguments for the importance of phytoplankton as a carbon source have alluded to the role of herbivorous zooplankton as intermediaries that are consumed directly or indirectly by juvenile fish or shrimps in the mangrove (Schwamborn, 1997; Bouillon et al., 2000; Chew et al., 2007).

Several studies have shown the dominance of zooplankton feeders among juvenile fish in the mangrove (Robertson & Duke, 1987; Blaber, 2000; Chew et al., 2007) where copepods are often the main food of small or young fishes (Robertson et al., 1988; Chew et al., 2007) and shrimps (Chong & Sasekumar, 1981). Copepod-dominated zooplanktons are more abundant in mangrove estuaries than in adjacent coastal waters (Robertson et al., 1988). In many cases, the higher abundance is correlated with the higher chlorophyll *a* concentration and primary production in the mangrove estuary (Robertson & Blaber, 1992). It has been argued that while phytoplankton production is low in mangrove creeks, it could be substantial in the more open estuaries (Chong, 2007). This view is consistent with studies based on stable isotope analysis indicating that penaeid shrimps sampled upstream to offshore become increasingly more dependent on phytoplankton carbon (Rodelli et al., 1984; Chong et al., 2001).

In the view that copepods are an important food source for young mangrove fishes, it is necessary to study their community structure and abundance in relation with the environment, to evaluate their contribution to mangrove trophodynamics and thus to coastal fisheries (see Blaber, 2007; Chong, 2007). Moreover, there are few studies on zooplankton ecology in the mangrove ecosystem worldwide (e.g., Grindley, 1984; Madhupratap, 1987; Robertson et al., 1988; McKinnon & Klumpp, 1998; Krumme & Liang, 2004). In Malaysian waters, published works on marine zooplankton or copepods are depauperate and sporadic (Sewell, 1933; Chong & Chua, 1975; Chua & Chong, 1975; Johan et al., 2002; Rezai et al., 2004, 2005; Yoshida et al., 2006), with only one involving mangrove (Oka, 2000). The present study therefore intends to contribute further knowledge of the ecological role of copepods in turbid-water mangrove habitats. The objectives are to determine the copepod community structure and abundance of

mangrove and adjacent coastal waters, and to relate copepod community attributes to the environmental factors.

Materials and methods

Study site

The general study site was located at the Matang Mangrove Forest Reserve (MMFR) on the west coast of Peninsular Malaysia (4°50'N, 100°35'E; Fig. 1). The MMFR is dominated by silvicultured *Rhizophora apiculata* Blume. The upper, middle, and lower regions of the complex interconnected estuaries of the Sangga rivers that were sampled for zooplankton were located 7, 3.5, and 0 km from the river mouth of Sangga Kecil (Table 1). The adjacent coastal waters were sampled at their nearshore and offshore sites located 8 and 16 km from the mouth of Sangga Kecil, respectively. The water depths are relatively shallow, the deepest water not exceeding 8 m. The hydrology of the Matang estuaries is dominated by semidiurnal tidal circulation. The tidal levels at MHWS, MHW, MLWN, and MLWS have been reported as 2.1, 1.5, 0.9, and 0.3 m above chart datum (Chong et al., 1999).

Field collection

Routine monthly sampling of zooplankton was carried out from May 2002 to October 2003 from the upper estuary to offshore waters (Fig. 1). Samplings were conducted during neap tides when the water parameters were less fluctuating (Chong et al., 1999). At each sampling station, physical parameters (salinity, temperature, pH, dissolved oxygen, and turbidity) were measured by a metered multi-parameter sonde (Model YSI 3800 and Hydrolab 4a). All water parameters were taken at 0.5 m depth. Rainfall data during sampling periods were obtained from the Malaysian Meteorological Department based on measurements recorded at Taiping, a town located 10 km to the east of MMFR. Chlorophyll *a* concentrations were measured using the fluorometric method (Parson et al., 1984) from July 2002 to October 2003.

Duplicate zooplankton samples were taken by 45 cm-diameter bongo nets (363 and 180 μ m) fitted with calibrated flow-meters. Two horizontal tows (0.5–1 m depth) were made at each station during

Fig. 1 Location map of sampling stations in the Matang Mangrove Forest Reserve and adjacent coastal waters. *Station 1* upper estuary, *Station 2* mid-estuary, *Station 3* lower estuary, *Station 4* nearshore water, *Station 5* offshore water

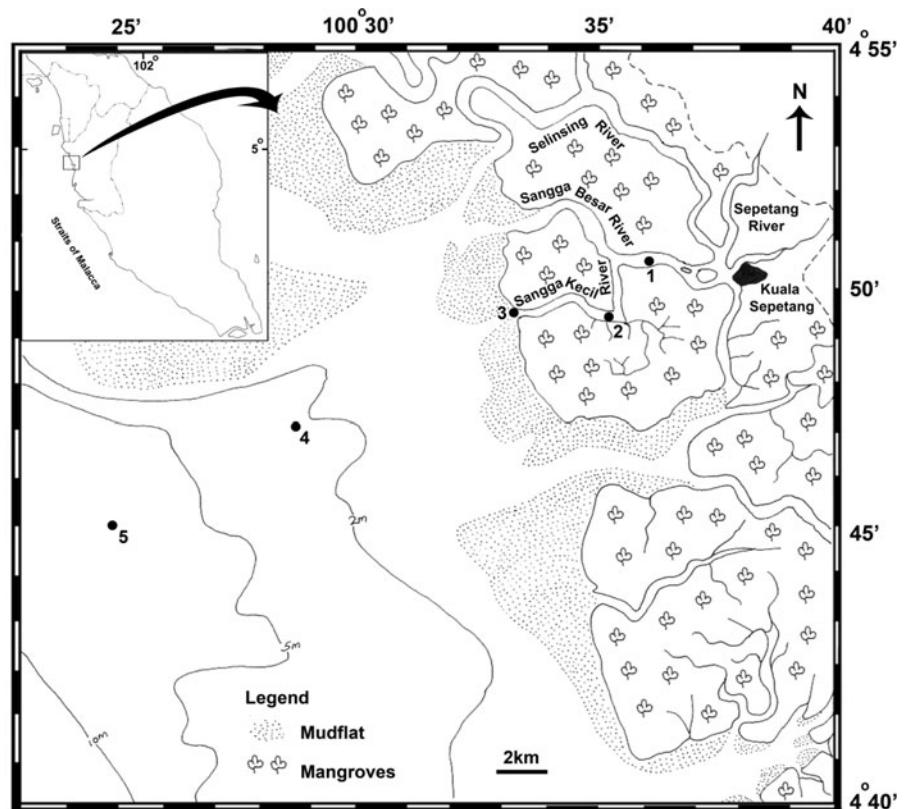


Table 1 Station location, water depth, number of species and composition of copepod population in Matang, Malaysia

Station	Location	Distance from river mouth (km)	Mean water depth (m)	Number of species identified	Percentage of copepod (%)	
					Adult	Juvenile
Upper estuary	4°50'N 100°36'E	-7	3.46	25	57.2	42.8
Mid-estuary	4°49'N 100°35'E	-3.5	7.25	29	49	51
Lower estuary	4°49'N 100°33'E	0	5.75	34	54.6	45.4
Nearshore	4°47'N 100°29'E	8	3.30	42	72.7	27.3
Offshore	4°45'N 100°25'E	16	7.04	39	66.4	33.6

Negative and positive distances indicate upstream and off shore directions, respectively

day, one on the seabound journey and the other on the return. Tow durations ranged between 3 and 10 min depending on net clogging. Collected zooplankton samples were preserved in 10% buffered formaldehyde in seawater and kept in 500 ml plastic bottles before subsequent analysis.

Only the 180 μ m-net samples were analyzed and the results reported here. Samples were gently and quickly wet sieved through stacked 1,000, 500, 250, and 125 μ m Endecott sieves using running tap water. The various fractions were immediately resuspended

in 80% alcohol in separate 100-ml vials. For enumeration, the samples were split between 1 and 8 times using a Folsom plankton splitter. Adult copepods were identified to species or the lowest possible level. Copepodids were identified to genus level. Juveniles that could not be identified were classified as unidentified copepodids or nauplii. Large copepods (>1 mm) were individually counted on a Petri dish. Small copepods (<1 mm) were subsampled using a 1 ml Stempel pipette before transferring them onto a 1 ml Sedgewick-Rafter cell for total counts.

Copepod abundance was calculated as number of individuals per m^3 (ind m^{-3}).

Data analyses

Univariate analysis

Species diversity was calculated for all adults and *Hemicyclops* copepodids using Shannon–Wiener diversity index (H') (Shannon, 1948) and Pielou's evenness (J') (Pielou, 1969). Two-way factorial ANOVA with unequal, but proportional replication was used to examine effects due to monsoon season (NE monsoon and SW monsoon) and station (upper estuary, mid-estuary, lower estuary, nearshore, and offshore) on the diversity index (H'), evenness (J'), copepod abundance [total, *Parvocalanus crassirostris* Dahl, *Acartia spinicauda* Mori, *Acartia* copepodid, *Oithona simplex* Farran, *Bestiolina similis* (Sewell), and *Euterpina acutifrons* (Dana)] and the various environmental variables (salinity, temperature, pH, dissolved oxygen, turbidity, and chlorophyll *a* concentration). If the ANOVA test was significant, Tukey HSD test was further conducted for multiple comparisons of the means. Data were first tested for normality and homogeneity of variance. Skewed data were either fourth rooted, $\log_{10}(x)$ (environmental variable) or $\log_{10}(x + 1)$ (copepod abundance) transformed. Kruskal–Wallis test was conducted if the variable (e.g., abundance of *Parvocalanus elegans* Andronov, *Metacalanus aurivilli* Cleve, and *Harpacticoida* sp1) did not fulfill parametric assumptions even after data transformation. Significance level at $\alpha = 0.05$ was applied to determine significant difference. All statistical analyses were conducted using Statistica Version 8 software on a PC.

Multivariate analysis

The relationships between copepod abundance and environmental variables were analyzed by RDA using the CANOCO 4 program. RDA is a constrained linear ordination method that assumes the species–environment relations are linear based on direct ordination (Ter Braak, 1994). We used RDA which is a short-gradient analysis because the copepod community variation in the study area was not wide, $<2\text{SD}$ (Ter Braak & Prentice, 1988). Eighty-eight

samples containing 23 copepod species (those that accounted for at least 0.2% of the total abundance at each sampling station) were related to six environmental parameters (salinity, pH, temperature, dissolved oxygen, turbidity, and chlorophyll *a* concentration). Copepod abundance was $\log_{10}(x + 1)$ transformed, while turbidity and chlorophyll *a* contents were $\log_{10}(x)$ transformed due to skewed data.

Results

Environmental parameters

Monthly rainfall at Taiping during the sampling period ranged from 67 to 650 mm (Fig. 2). Mean total rainfall (221 mm) and mean number of rainy days (17 days) during the SW monsoon period were relatively lower than that (416 mm, 25 days) during the NE monsoon. The rainfall pattern, however, did not show a well-defined dry and wet seasons (Fig. 2).

Mean station salinity ranged from 20.4 ± 3.7 ppt to 30.5 ± 1.2 ppt from upper estuary to offshore waters (Fig. 3a; Table 2). Salinity was significantly higher ($P < 0.01$) during the SW monsoon season than NE monsoon season, but there were no significant interaction effects between monsoon season and station. Mean pH values of near neutral (7.2) recorded at the upper estuary increased to 8.0 in offshore waters. Mean DO values also increased in the offshore direction ($4.8\text{--}6.0 \text{ mg l}^{-1}$). Mean turbidity values were highest at the river mouth (35.6 NTU) generally decreased in both directions, but the clearest water was observed offshore (15.2 NTU). Mean water temperature of the five stations were generally similar ranging between 30 and 31°C , while mean monthly temperature at station was rather consistent at $<1.5^\circ\text{C}$ fluctuation during the sampling period (Table 2). Water temperatures of both mangrove and adjacent coastal waters were not significantly different between the two monsoon seasons (Fig. 3b).

Phytoplankton biomass as indicated by mean chlorophyll *a* concentration was higher at the mangrove stations (21.0 , 20.2 , and $22.8 \mu\text{g l}^{-1}$) than at the nearshore ($12.3 \mu\text{g l}^{-1}$) or offshore ($9.2 \mu\text{g l}^{-1}$) stations (see Table 2). After pooling the above data, the mean chlorophyll *a* concentration was found to be significantly higher ($P < 0.01$) in the mangrove

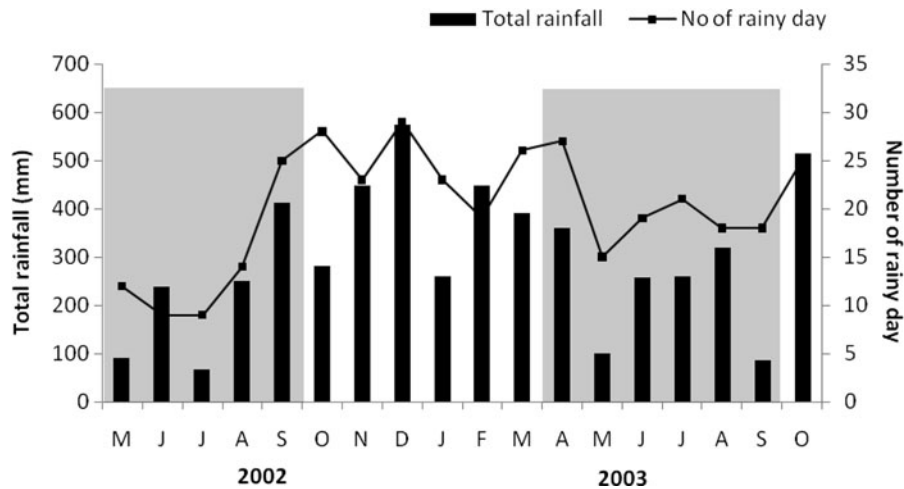


Fig. 2 Monthly total rainfall and number of rainy days recorded from May 2002 to October 2003 at Taiping, located 10 km east of the study site. *Shaded* region indicates SW

monsoon period (April–September); *unshaded* region indicates NE monsoon period (October–March)

estuary ($40.1 \pm 21.9 \mu\text{g l}^{-1}$) than adjacent coastal waters ($26.8 \pm 7.7 \mu\text{g l}^{-1}$), and in the NE monsoon ($21.3 \pm 21.7 \mu\text{g l}^{-1}$) than in the SW monsoon ($14.1 \pm 8.5 \mu\text{g l}^{-1}$) period. Phytoplankton blooms apparently occurred in the mangrove estuary with a major peak in January 2003 (Fig. 3c), following heavy rainfall in December 2002.

Spatial variation of copepod abundance and composition

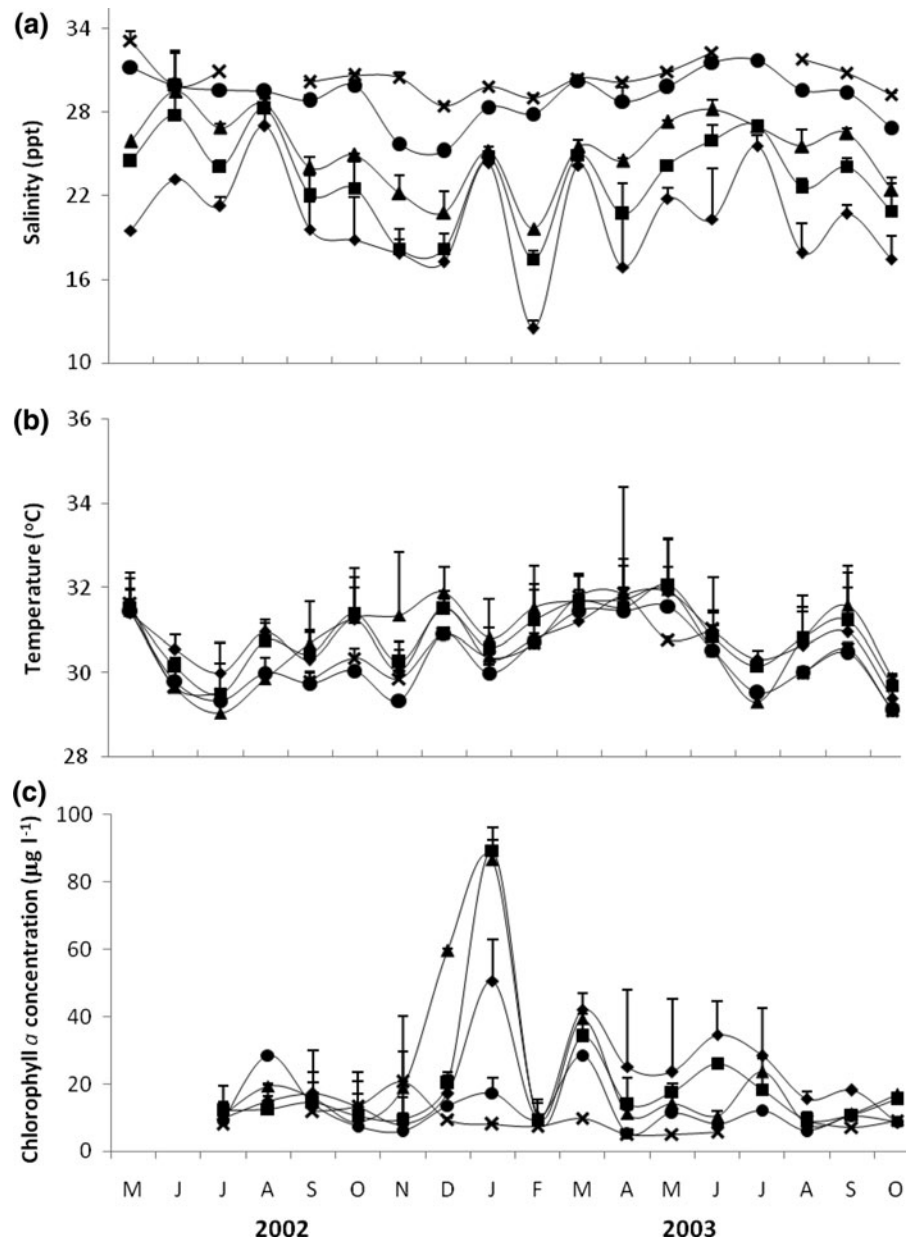
Mean zooplankton density estimated for the mangrove estuary and adjacent coastal waters over the sampling period were $26,533 \text{ ind m}^{-3}$ ($\text{SD} \pm 23,089 \text{ ind m}^{-3}$) and $30,945 \text{ ind m}^{-3}$ ($\text{SD} \pm 56,643 \text{ ind m}^{-3}$), respectively. Copepods constituted at least 47% of the zooplankton at all stations. Density of copepods at the five stations ranged from 3,030 to $62,650 \text{ ind m}^{-3}$ (mean = $17,417 \text{ ind m}^{-3}$, $\text{SD} \pm 13,223 \text{ ind m}^{-3}$), with the lowest density recorded at mid-estuary in May 2003 and the highest at upper estuary in December 2002 (Fig. 4a, b). However, mean density of total copepods increased from the upper estuary ($15,572 \pm 20,171 \text{ ind m}^{-3}$) to nearshore waters ($20,311 \pm 12,892 \text{ ind m}^{-3}$), and decreased toward offshore waters ($12,330 \pm 11,046 \text{ ind m}^{-3}$; Fig. 5; Table 2).

A total of 48 species of copepods were recorded. The highest number of identified copepod taxa was

obtained from the nearshore station (42 taxa) followed by offshore (39 taxa) station. In mangrove waters, the lower estuary, mid-estuary, and upper estuary each recorded 34, 29, and 25 taxa, respectively (Table 1). Shannon–Wiener diversity index (H') and Pielou's evenness (J') were significantly lowest ($P < 0.01$) at the upper estuary as compared to the other four stations (Table 2). Nearshore and offshore copepods were mainly adults, constituting 73 and 66% of the total copepod abundance, respectively. Juvenile copepods (copepodid and nauplius stages) of mainly *Acartia* copepodids constituted 43–51% of the total copepod abundance in mangrove waters (Table 1).

Dominant species that comprised at least 5% of the total abundance or present in at least one station were *P. crassirostris*, *A. spinicauda*, *O. simplex*, *B. similis*, and *E. acutifrons*. The small calanoid copepod, *P. crassirostris* comprised 20–32% of the copepod population and was present in all samples collected during the study (100% occurrence; Table 3). *P. crassirostris* was also the most abundant species at all sampling stations except in mid-estuary and nearshore waters which were dominated by *Acartia* copepodids and *O. simplex*, respectively (Fig. 5). Copepodids of *Parvocalanus* constituted 6–12% of the total abundance and were absent in only a few samples from the upper estuary. *P. crassirostris* abundance showed that no significant difference

Fig. 3 Monthly mean and standard deviation (vertical bar) of (a) salinity, (b) temperature and (c) chlorophyll *a* concentrations recorded at five sampling stations. Filled diamond Upper estuary; filled square mid-estuary; filled triangle lower estuary; filled circle nearshore; times offshore



among sampling stations suggesting that the euryhaline species could tolerate a wider range of salinity (Fig. 5). *Acartia* copepodid abundance was always higher than their adults at all stations (Table 3). Juvenile stages of *Acartia* were as dominant as *P. crassirostris*, but they were more confined inside mangrove waters ($P < 0.01$; Table 2). Mean total abundance of *Acartia* copepodids ($6,129 \pm 5,866 \text{ ind m}^{-3}$) exceeded *P. crassirostris* ($4,211 \pm 4,196 \text{ ind m}^{-3}$) at mid-estuary (Table 3). A similar

distribution pattern was observed for *A. spinicauda* with higher abundance in mangrove than coastal waters (Fig. 5). In contrast, *O. simplex* showed preference for higher salinity water although it was sampled at all stations. The abundance of *O. simplex* was significantly higher at the river mouth to coastal stations ($P < 0.01$) than at the upper and mid-estuary (Table 2). It was more abundant than even *P. crassirostris* in nearshore waters (Fig. 5; Table 3). A similar trend of distribution as *O. simplex* was also

Table 2 Summary results of two-way ANOVA and post-hoc Tukey HSD tests on various environmental variables, biological indices and selected copepod abundance, with respect to station, season and their interaction

Variable	n	Source of variation										Station x Season P-level
		Station					Season					
		Upper estuary 36 (32)	Mid-estuary 36 (32)	Lower estuary 36 (32)	Nearshore 36 (32)	Offshore 32 (28)	P-level	SW 106 (86)	NE 70	P-level		
Salinity (‰)	Mean	20.4 ^a	23.2 ^b	25.2 ^c	29.1 ^d	30.5 ^d	<0.001**	26.6	24.1	<0.001**	0.198	
	±SD	3.7	3.3	2.7	1.8	1.2		4.1	4.9			
pH	Mean	7.2 ^a	7.5 ^b	7.6 ^c	7.9 ^d	8.0 ^d	<0.001**	7.7	7.6	<0.001**	0.014*	
	±SD	0.3	0.2	0.2	0.1	0.1		0.3	0.4			
Dissolved oxygen (mg l ⁻¹)	Mean	4.8 ^a	5.2 ^{a,b}	5.6 ^{b,c}	6.0 ^c	6.0 ^c	<0.001**	5.8	5.1	<0.001**	0.011*	
	±SD	1.5	1.2	1.1	0.8	0.6		0.9	1.4			
Turbidity (NTU)	Mean	29.9 ^a	30.9 ^a	35.6 ^a	28.5 ^a	15.2 ^b	0.007**	20.0	40.7	<0.001**	0.508	
	±SD	38.5	43.9	71.2	22.5	14.3		15.9	64.2			
Temperature (°C)	Mean	30.8 ^a	30.9 ^a	30.8 ^a	30.3 ^a	30.5 ^a	0.025*	30.6	30.7	0.736	0.335	
	±SD	1.0	0.8	1.1	0.8	0.8		0.9	0.9			
Chlorophyll <i>a</i> (µg l ⁻¹)	Mean	21.0 ^a	20.2 ^{a,b}	22.8 ^a	12.3 ^{b,c}	9.2 ^c	<0.001**	14.1	21.3	0.009**	0.093	
	±SD	15.5	19.6	21.8	7.2	4.6		8.5	21.7			
Δ Diversity index (H')	Mean	1.17 ^a	1.39 ^b	1.55 ^b	1.53 ^b	1.49 ^b	<0.001**	1.52	1.28	<0.001**	0.088	
	±SD	0.35	0.34	0.28	0.36	0.29		0.31	0.36			
Evenness (J')	Mean	0.54 ^a	0.60 ^{a,b}	0.63 ^b	0.57 ^{a,b}	0.56 ^a	0.001**	0.62	0.53	<0.001**	0.120	
	±SD	0.15	0.12	0.10	0.11	0.10		0.11	0.12			
Copepod abundance												
Total copepods	Mean	15,572 ^a	18,796 ^{a,b}	19,759 ^{a,b}	20,311 ^b	12,330 ^a	0.003**	13,115	23,933	<0.001**	0.960	
	±SD	20,171	15,040	16,195	12,892	11,046		11,381	18,675			
<i>Parvocalanus crassirostris</i>	Mean	4,871	4,211	4,516	4,043	3,174	0.327	2,796	6,290	<0.001**	0.137	
	±SD	9,458	4,196	4,590	3,791	3,835		3,105	7,586			
<i>Acartia spinicanda</i>	Mean	1,103 ^a	1,374 ^a	1,157 ^a	300 ^{a,b}	112 ^b	<0.001**	505	1,310	0.001**	0.373	
	±SD	3,340	2,872	1,972	363	137		1,423	3,008			
<i>Acartia copepodid</i>	Mean	4,501 ^a	6,129 ^a	4,251 ^a	605 ^b	313 ^b	<0.001**	2,488	4,340	<0.001**	0.884	
	±SD	6,393	5,866	4,329	833	485		4,064	5,851			
<i>Oithona simplex</i>	Mean	843 ^a	1,251 ^{a,b}	2,462 ^c	5,720 ^d	1,701 ^{b,c}	<0.001**	1,575	3,678	<0.001**	0.420	
	±SD	1,973	2,268	3,431	6,993	2,707		2,473	5,880			

Table 2 continued

Variable	Source of variation										
	Station					Season					Station x Season
	Upper estuary 36 (32)	Mid-estuary 36 (32)	Lower estuary 36 (32)	Nearshore 36 (32)	Offshore 32 (28)	P-level	SW 106 (86)	NE 70	P-level	P-level	
<i>Bestiolina similis</i>	Mean	248 ^a	275 ^{ab}	437 ^{b,c}	1,102 ^c	607 ^c	492	592	0.118	0.412	
	±SD	472	377	484	1,536	665	623	1,165			
<i>Euterpina acutifrons</i>	Mean	12 ^a	63 ^b	221 ^b	1,865 ^c	1,037 ^c	394	988	0.321	0.276	
	±SD	37	140	333	3,362	1,255	677	2,631			

n = sample size for all parameters except chlorophyll a in parentheses; Δ diversity index (H') computed on log-base e ; homogeneous groups indicated by *superscripts* a, b, c and d
* Significance at $P < 0.05$, ** significance at $P < 0.01$

observed for *B. similis* and its juveniles (Fig. 5). *E. acutifrons* preferred nearshore (9%) and offshore (8%) waters than mangrove waters (<1%; Fig. 5).

Tortanus barbatus (Brady) and *Tortanus forcipatus* (Giesbrecht) each constituted less than 1% of the overall copepod abundance, but copepodids of *Tortanus* comprised 5% of the total copepod abundance in nearshore waters (Fig. 5). *Tortanus* copepodids were frequently sampled in nearshore and offshore stations with >90% of occurrence (Table 3). Other copepods, such as *Oithona dissimilis* Lindberg, *Oithona aruensis* Früchtl, *Acartia* sp1, copepodids of *Pseudodiaptomus*, *Oithona attenuata* Farran, and copepodids of Pontellidae, were also frequently collected. The former first four taxa were more abundant in estuarine waters whereas the Pontellidae mainly occurred in offshore waters (Table 3).

Temporal variation of copepod abundance and composition

The abundance of copepods was significantly higher ($P < 0.01$) during the NE monsoon period which experienced a higher rainfall (Table 2). Seasonal variation in copepod abundance was markedly observed at the upper estuary with two large peaks in December 2002 and October 2003 (Fig. 4a) that coincided with the period of heaviest rainfall. Upper estuary copepods sampled monthly rarely exceeded 20,000 ind m^{-3} , but densities in these months were much higher at ca. 60,000 ind m^{-3} . Peak abundance was also exhibited at mid-estuary to offshore stations during NE monsoon particularly in November 2002, February 2003, and October 2003 (Fig. 4b–e) concurrently the months of heavy rainfall (see Fig. 2). Copepod abundance was scarce in June and August 2002 and in May and June 2003 (Fig. 4). These were the months of lower rainfall (see Fig. 2). Although copepod abundance was relatively lower during SW monsoon, new copepod recruits first appeared in September 2002 and August 2003 (Fig. 4b–e), and their numbers soon increased thereafter with the arrival of heavier rain.

Variations in copepod abundance were generally influenced by the seasonal change of dominant species. The abundance of copepods in mangrove waters was strongly dependent on the dominant genera, *Acartia* and *Parvocalanus*. *P. crassirostris*

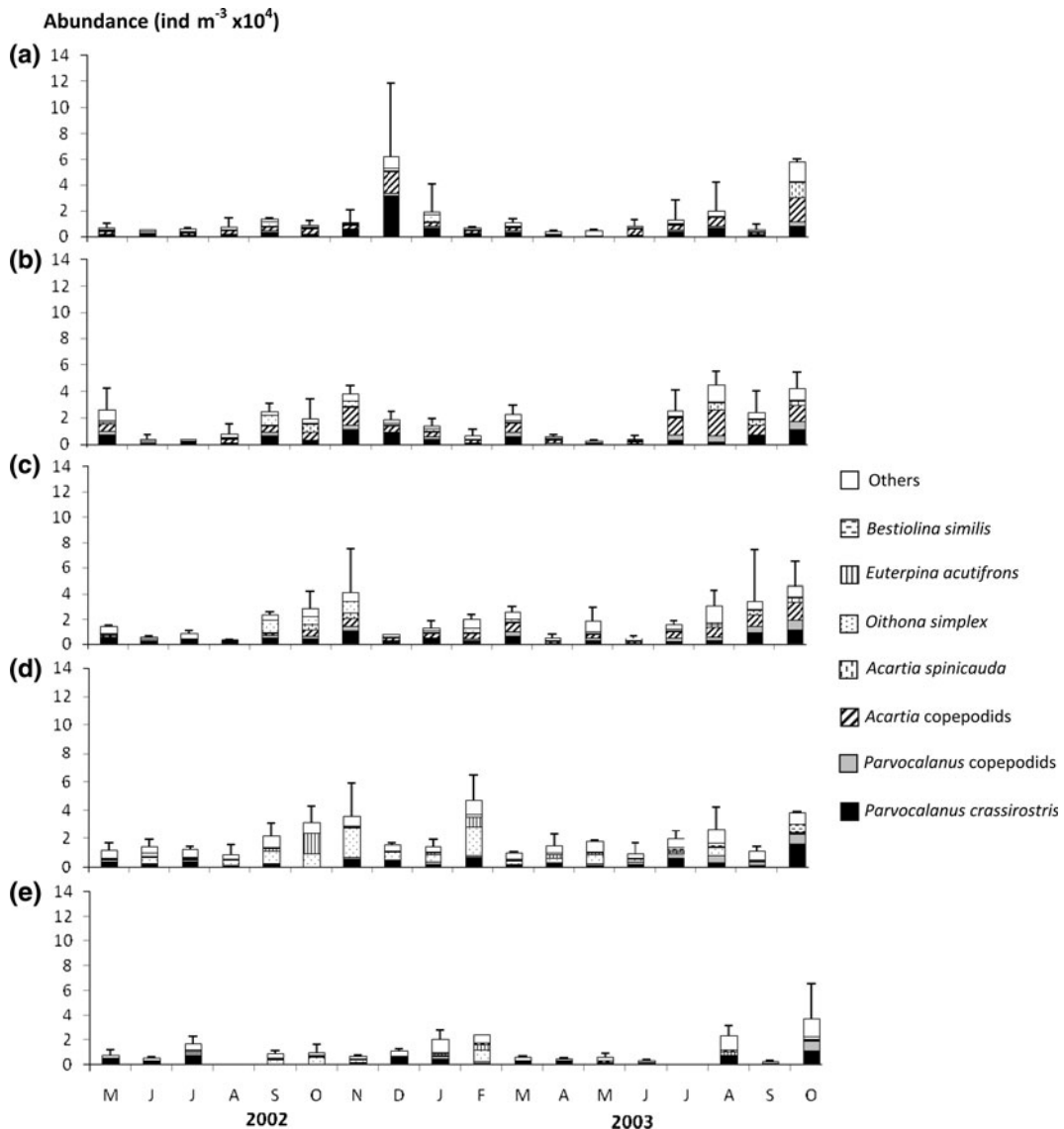


Fig. 4 Monthly composition of major copepod taxa by station, from May 2002 to October, 2003. **(a)** upper estuary; **(b)** mid-estuary; **(c)** lower estuary; **(d)** nearshore water; **(e)** offshore

water. Only the five most abundant taxa of each station are shown. “Others” grouped the remainder species. *Error bar* indicates SD of total abundance

was significantly more abundant ($P < 0.01$) during the NE monsoon than SW monsoon (Table 2). Similarly, the abundance of *A. spinicauda* and copepodids varied seasonally and were significantly more abundant ($P < 0.01$) during the NE monsoon period (Fig. 4; Table 2). The coastal species, *O. simplex*, was also significantly more abundant ($P < 0.01$) during the NE monsoon period particularly in November 2002 and February 2003 (Fig. 4;

Table 2). The abundance of *E. acutifrons* and *B. similis* was not seasonally affected. The higher densities of the dominant species had resulted in a significantly lower ($P < 0.01$) diversity index and evenness during the NE monsoon than in the SW monsoon (see Fig. 6; Table 2). No significant interaction effects ($P > 0.05$) between station and monsoon period were detected for copepod abundances and diversity indexes (Table 2).

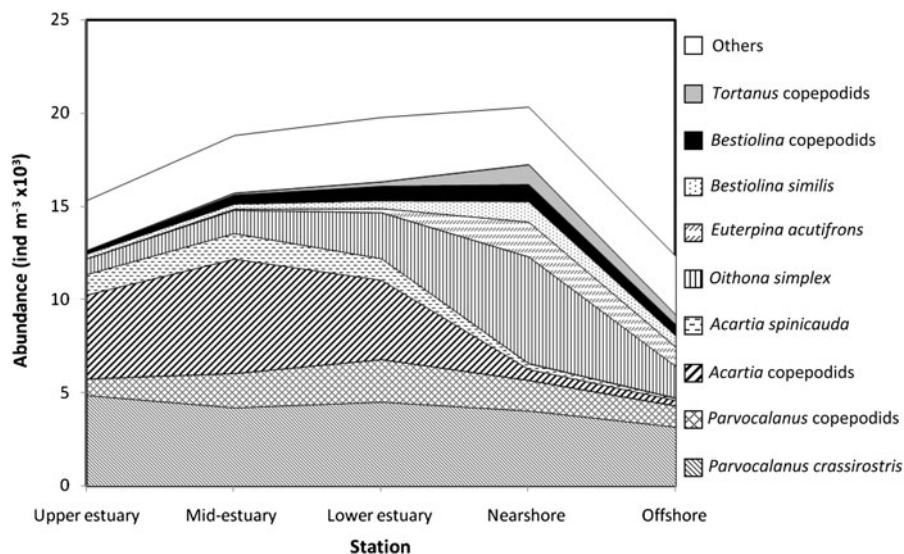


Fig. 5 Mean abundance of copepod species (those comprising >5% of total abundance) by sampling stations

Species–environment relationships

The relationship between copepod species and environmental parameters is shown in the RDA ordination diagrams in Fig. 6. The first two axes explained 88.6% of the variance in the correlation of species–environmental parameters. Stations in mangrove water (1, 2, and 3) were generally positively correlated with higher turbidity values and chlorophyll *a* concentrations (positive direction on axis 1), but negatively correlated with lower salinity and pH values (negative direction on axis). Coastal stations (4 and 5), however, showed the exact opposite (Fig. 6a).

Although most of the copepod species samples were present at all stations, they can be generally classified into stenohaline, estuarine, and euryhaline species based on their relative abundance along the salinity gradient over spatial and temporal scales. The abundance of four estuarine species, *A. spinicauda*, *Acartia* sp1, *O. dissimilis*, and *O. aruensis* were negatively correlated with salinity and pH indicating that these species preferred lower salinity although they were also found in nearshore and offshore waters (see Fig. 6b; Table 3). Nevertheless, 12 out of 23 species were closely associated with higher salinity and pH suggesting that these copepods were stenohaline species. The four major stenohaline species that were only present at the lower estuary and further

offshore stations were *Paracalanus aculeatus* Giesbrecht, *Acartia erythraea* Giesbrecht, *Corycaeus andrewsi* Farran, and *Acrocalanus gibber* Giesbrecht (see Table 3). Other stenohaline species that were sporadically found inside the estuary included the calanoids, *Centropages dorsispinatus* Thompson & Scott, *T. barbatus*, *T. forcipatus*, the cyclopoids, *Oithona attenuata* Farran, *Oithona brevicornis* Giesbrecht, *Hemicyclops* sp1, *Pseudomacchiron* sp1, and the harpacticoids, *E. acutifrons*, and *Microsetella norvegica* Dana.

The euryhaline species were oriented closer to axis 2 in the positive direction. Within the group, the species that correlated with higher salinity were *O. simplex*, *B. similis*, and *M. aurivilli*. The arrow orientations of *P. crassirostris*, *P. elegans*, and Harpacticoida sp1 were almost perpendicular to the salinity gradient implying that salinity did not have significant effect on their abundance. However, these species seemed to be more associated with higher turbidity (Fig. 6b). Parametric and non-parametric tests further revealed that no significant difference in abundance among stations for euryhaline species except *O. simplex* and *B. similis* which were more abundant in the coastal stations (Table 3).

Copepod community of the upper estuary (1) appeared quite distinct from those of the nearshore and offshore waters (4 and 5) (see Fig. 6b). The monsoon had an effect on the copepod community of

Table 3 Mean abundance (ind m⁻³), relative abundance (% Rel), and occurrence (% Occ) of copepods recorded from the upper estuary to offshore waters

Taxon	Station															
	Upper estuary			Mid-estuary			Lower estuary			Nearshore			Offshore			
	Mean	% Rel	% Occ	Mean	% Rel	% Occ	Mean	% Rel	% Occ	Mean	% Rel	% Occ	Mean	% Rel	% Occ	
Adult																
<i>Parvocalanus crassirostris</i> Dahl	4,871	31.8	100	4,211	22.4	100	4,516	22.9	100	4,043	19.9	100	3,174	25.7	100	
<i>Acartia spinicauda</i> Mori	1,103	7.2	100	1,374	7.3	94	1,157	5.9	97	300	1.5	100	112	0.9	88	
<i>Oithona simplex</i> Farran	843	5.5	92	1,251	6.7	92	2,462	12.5	100	5,720	28.2	100	1,701	13.8	100	
<i>Parvocalanus elegans</i> Andronov	618	4.0	33	229	1.2	14	151	0.8	31	73	0.4	36	106	0.9	13	
<i>Oithona dissimilis</i> Lindberg	569	3.7	100	568	3.0	100	484	2.4	86	60	0.3	19	+	+	3	
<i>Oithona arvensis</i> Früchtl	287	1.9	97	391	2.1	94	664	3.4	100	214	1.1	69	93	0.8	22	
<i>Bestiolina similis</i> (Sewell)	248	1.6	72	275	1.5	75	437	2.2	92	1,102	5.4	92	607	4.9	100	
<i>Acartia</i> sp1	175	1.1	89	774	4.1	97	394	2.0	97	+	+	8	+	+	6	
<i>Euterpina acutifrons</i> (Dana)	+	+	31	63	0.3	69	221	1.1	69	1,865	9.2	100	1,037	8.4	97	
<i>Oithona attenuata</i> Farran	+	+	11	+	+	14	56	0.3	25	300	1.5	78	392	3.2	91	
<i>Centropages dorsispinatus</i> Thompson & Scott	+	+	11	+	+	25	+	+	25	326	1.6	69	123	1.0	69	
<i>Paracalanus aculeatus</i> Giesbrecht	+	+	6	+	+	+	+	+	6	55	0.3	42	246	2.0	53	
<i>Oithona brevicornis</i> Giesbrecht	+	+	3	+	+	17	+	+	6	+	+	11	228	1.9	47	
<i>Microsetella norvegica</i> Dana	+	+	3	+	+	+	+	+	25	132	0.7	53	20	0.2	41	
<i>Corycaeus andrewsi</i> Farran	+	+	6	+	+	17	+	+	19	118	0.6	56	121	1.0	75	
<i>Pseudomacrochiron</i> sp1	+	+	31	+	+	56	45	0.2	36	52	0.3	33	+	+	13	
<i>Tortanus barbatus</i> (Brady)	+	+	3	+	+	6	+	+	61	84	0.4	86	30	0.2	66	
<i>Metacalanus aurivilli</i> Cleve	+	+	6	+	+	25	+	+	6	59	0.3	17	+	+	9	
<i>Tortanus forcipatus</i> (Giesbrecht)	+	+	14	+	+	22	84	0.4	33	57	0.3	69	22	0.2	59	
Harpacticoida sp1	+	+	6	+	+	8	+	+	11	35	0.2	36	+	+	6	
<i>Hemicyclops</i> sp1	+	+	6	+	+	+	+	+	11	39	0.2	36	49	0.4	69	
<i>Acartia erythraea</i> Giesbrecht	+	+	3-25	+	+	3-28	+	+	+	31	0.2	28	+	+	41	
<i>Acrocalanus gibber</i> Giesbrecht	+	+	3-25	+	+	3-28	+	+	+	54	0.3	3-56	70	0.6	3-66	
Other adults																
Nauplius and copepodid																
<i>Acartia</i> spp.	4,501	29.4	100	6,129	32.6	100	4,251	21.5	100	605	3.0	97	313	2.5	97	
<i>Parvocalanus</i> spp.	881	5.8	97	1,828	9.7	100	2,272	11.5	100	1,629	8.0	100	1,129	9.2	100	
Unidentified nauplii	710	4.6	100	566	3.0	100	720	3.6	100	612	3.0	100	448	3.6	100	
<i>Bestiolina</i> sp.	172	1.1	69	497	2.6	83	778	3.9	92	922	4.5	92	573	4.6	91	

Table 3 continued

Taxon	Station														
	Upper estuary			Mid-estuary			Lower estuary			Nearshore			Offshore		
	Mean	% Rel	% Occ	Mean	% Rel	% Occ	Mean	% Rel	% Occ	Mean	% Rel	% Occ	Mean	% Rel	% Occ
<i>Pseudodiaptomus</i> spp.	172	1.1	86	278	1.5	97	279	1.4	86	110	0.5	69	86	0.7	72
<i>Oithona</i> spp.	95	0.6	69	163	0.9	72	323	1.6	69	131	0.6	81	75	0.6	72
<i>Tortanus</i> spp.	26	0.2	42	92	0.5	72	225	1.1	89	1,056	5.2	97	543	4.4	94
Pontellidae spp.	+	+	19	29	0.2	47	59	0.3	53	256	1.3	89	495	4.0	100
Other juveniles	+(2)	+	3–6	+(3)	+	3–6	55 (6)	0.3	6–19	227 (7)	1.1	3–36	478 (10)	3.9	3–72

“+” indicates present but constituted <0.2% of relative abundance; number of taxa of grouped copepods in parentheses

the lower estuary (3) where a seasonal shift in community structure was evident. For instance, stenohaline and euryhaline species dominated in the lower estuary during the dry period from June to September (dotted line arrows joining station 3), but the community soon changed to one dominated by estuarine species with the onset of the wet period from October to January (dotted line arrows joining station 3 in boldface). Neritic copepods invaded the lower estuary and reached the upper estuary in the driest months of June to August (indicated by polygon enclosing stations 1 and 2) when high salinity water penetrated upstream.

Discussion

Copepod composition and community structure

Acartiidae, Paracalanidae, and Oithonidae were the predominant copepod taxa in the MMFR and adjacent waters, comprising 70–98% of total copepod population. The estuarine species, *A. spinicauda* and *Acartia* sp1, were mostly sampled at their copepodid stages. Low abundance of adults as compared to copepodids implied the recruitment of new generation and juvenile mortality. McKinnon & Klumpp (1998) found that the larger species, such as *Acartia*, were rare in a mangrove estuary in Queensland, Australia. The distribution of *Acartia* species is affected by salinity and temperature (Ueda, 1987; Cervetto et al., 1999; Gaudy et al., 2000). Yoshida et al. (2006) suggested that *Acartia pacifica* Steuer prefers water of higher salinity and lower temperature as opposed to *A. spinicauda*. In our study, *A. erythraea*, which was found in more saline and relatively lower temperature water, was not observed in the Matang estuary over the sampling period. On the other hand, *Acartia* sp.1 was more confined to mangrove waters, while *A. spinicauda* was more dispersed including to adjacent coastal waters. *A. spinicauda*, which is known to have a broad salinity tolerance, was the most abundant Acartiidae sampled from the MMFR and adjacent waters.

Parvocalanus crassirostris is widely distributed from the upper mangrove estuary to offshore waters. This species has been identified as a common species of Australian mangroves as well as the Great Barrier Reef lagoons (McKinnon & Klumpp, 1998). The

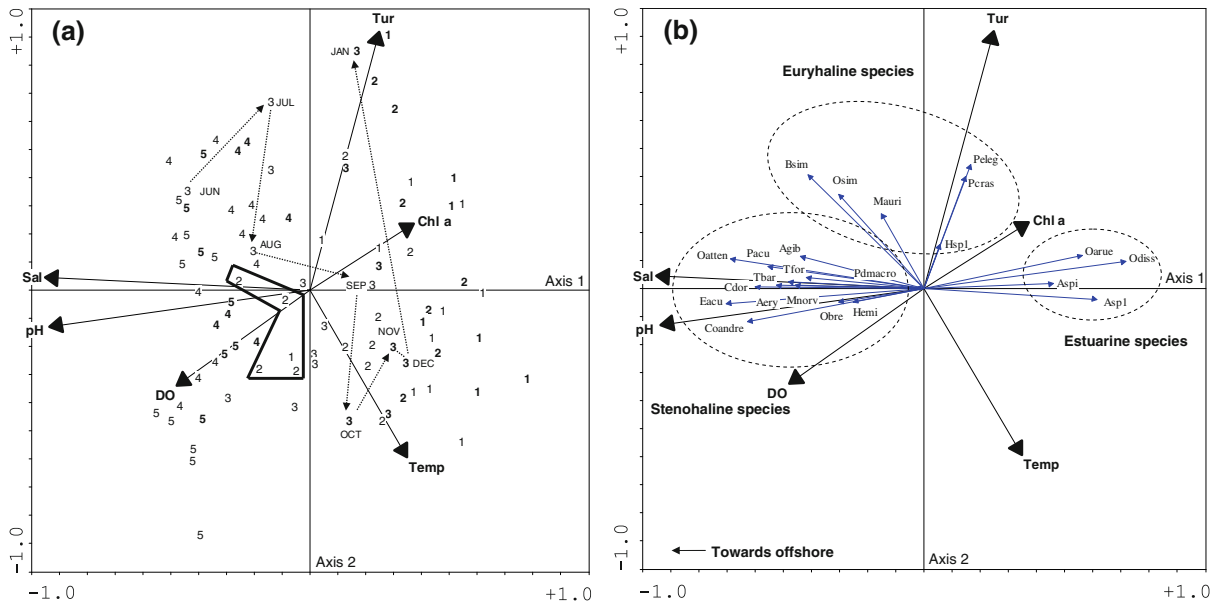


Fig. 6 RDA ordination diagrams showing (a) biplots of environmental parameters (large arrow heads) and station samples (1–5), and (b) biplots of environmental parameters (large arrow heads) and copepod taxa (small arrow heads). Dotted line arrows in (a) show seasonal shift of environmental parameters and copepod community structure from June to August 2002 (dry period) and from October to January 2003 (wet period) in the lower estuary. Polygon enclosing upper stations (1 and 2) indicates dry period from June to August 2002/2003. Numbers indicate sampled stations at: 1 upper estuary, 2 mid-estuary, 3 lower estuary, 4 nearshore water, and 5 offshore water. Bold face numbers indicate sampling during NE monsoon, while regular numbers indicate sampling during

SW monsoon. Abbreviations used: Sal, salinity; DO, dissolved oxygen; Temp, temperature; Tur, turbidity; Chl a, chlorophyll a concentrations; Aery, *Acartia erythraea*; Aspi, *A. spinicauda*; Asp1, *Acartia* sp1; Pcras, *Parvocalanus crassirostris*; Peleg, *P. elegans*; Agib, *Acrocalanus gibber*; Bsim, *Bestiolina similis*; Pacu, *Paracalanus aculeatus*; Mauri, *Metacalanus aurivilli*; Tbar, *Tortanus barbatus*; Tfor, *T. forcipatus*; Cdor, *Centropages dorsispinatus*; Oarue, *Oithona aruensis*; Oatten, *O. attenuata*; Obre, *O. brevicornis*; Odiss, *O. dissimilis*; Osim, *O. simplex*; Coandre, *Corycaeus andrewsi*; Hemi, *Hemicyclops* sp1; Pdmacro, *Pseudomacrochiron* sp1; Eacu, *Euterpina acutifrons*; Hsp1, Harpacticoida sp1; Mnorv, *Microsetella norvegica*

species is considered eurythermal and euryhaline species, since they are found to inhabit water of 3.4–55 ppt and 1–30°C (Lawson & Grice, 1973). Due to its ability to adapt to a wide range of salinity and temperature, *P. crassirostris* has successfully dominated the copepod community of MMFR and adjacent waters. The closely similar *P. elegans* is also, but sporadically present, while *B. similis* prefers more saline coastal waters. The three Paracalanidae species have been reported to be among the dominant species of copepod found in the Straits of Malacca (Rezai et al., 2005).

The cyclopoid, *Oithona* is commonly found in the Malaysian waters (Chong & Chua, 1975). *O. simplex*, *O. attenuata*, *Oithona plumifera* Baird, *Oithona rigida* Giesbrecht, and *Oithona nana* Giesbrecht are commonly encountered (Chua & Chong, 1975; Rezai et al., 2004). However, only the former two were

commonly collected in MMFR and its adjacent waters. As also reported by Oka (2000), the estuarine oithonids, *O. dissimilis*, and *O. aruensis* are also common in MMFR waterways, but have not been reported in the Straits of Malacca by Rezai et al. (2004) and Chua & Chong (1975). In the present study, *O. brevicornis* and *O. rigida* were both restricted to more saline waters. However, the latter was rare although this species was found to be abundant in the Straits of Malacca (Chua & Chong, 1975; Rezai et al., 2004).

Our samples were generally composed of planktonic copepods. The so-called “Saphirella-like” copepodids of *Hemicyclops* were occasionally collected in both mangrove and adjacent coastal waters, but were more abundant in the latter. The genus *Hemicyclops* with its first-stage copepodid occurring as plankton is closely associated with various benthic

borrowers that are normally found in the estuary, coastal inlet, and mudflat (Boxshall & Halsey, 2004; Itoh, 2006; Itoh & Nishida, 2007). Thus, as in our study, *Hemicyclops* copepodids were more abundant in nearshore waters close to coastal mudflats. Nevertheless, the ecology of this genus in the mudflat region of MMFR has not been documented before. Similarly, *Pseudomacrochiron* sp1 which is commonly associated with scyphozoans and hydrozoans (Boxshall & Halsey, 2004) was occasionally present in our samples.

Copepod abundance

Copepods dominate both mangrove and coastal waters in Matang, and they are numerically more abundant than in offshore waters. Previous studies in the Straits of Malacca show that copepod abundance was higher in coastal waters (Chong & Chua, 1975; Chua & Chong, 1975; Rezai et al., 2004) than in offshore waters. Similarly, copepod-dominated zooplanktons in mangrove estuaries of India and Australia have also been reported to be more abundant than in offshore waters (Madhupratap, 1987; Robertson et al., 1988; McKinnon & Klumpp, 1998). The abundance of copepod can be as high as 60,000 ind m⁻³ in Matang during the NE monsoon season. In comparison, the deeper waters of the Straits of Malacca yielded a mean total copepod abundance of only 3,000 ind m⁻³ (Rezai et al., 2004). In Cochin backwaters, India, a density of ca. 55,000 ind m⁻³ of copepods was recorded by Tranter & Abraham (1971), while an even higher abundance of 286,000 ind m⁻³ had been recorded from the Vellar estuary, India, by Subbaraju & Krishnamurthy (1972). However, the documented copepod abundance may not be comparable among studies since plankton nets of different mesh sizes were used (Robertson et al., 1988; McKinnon & Klumpp, 1998). We used a 180 µm mesh size net, while others used nets of smaller mesh sizes.

The abundance of copepod nauplii, copepodids, and highly nocturnal copepods are likely to be underestimated in the present study, since a 180 µm mesh size net was used to sample copepods at the surface during day time. We rarely observed *Pseudodiaptomus* spp. in our daytime samples although they were sampled at the surface during night (not

reported in this study). However, fish diet analysis showed that large numbers of *Pseudodiaptomus annandalei* Sewell were eaten by small or juvenile demersal fish during day time (Chew et al., 2007). This suggests that such markedly nocturnal behavior may be a response to predation.

The abundance of copepods is closely associated with the physical–chemical parameters of their habitats. Copepod abundance has been reported to vary seasonally in tropical mangrove and coastal waters with higher abundance in the wet season or after the monsoonal flush (Madhupratap, 1987; Robertson et al., 1988; Osore, 1992; McKinnon & Klumpp, 1998; Krumme & Liang, 2004). Similarly in MMFR waterways and shallow coastal waters, copepod abundance is affected by a rainfall pattern that is monsoon-dictated. The abundance of copepod appears to peak after heavy rainfall. However, in the deeper waters of the Straits of Malacca, there appears to be no significant difference in copepod abundance between the monsoon seasons (Rezai et al., 2004). This is attributable to the stable physical and chemical conditions of the deep water as compared to the variable estuarine and coastal conditions.

The abundance of zooplankton in the mangrove and nearshore waters may be related to primary production (see Robertson & Blaber, 1992) driven by phytoplankton, benthic microalgae, and mangrove. Phytoplankton biomass has been reported to be closely related to water nutrient level in a tropical mangrove swamp in Australia during the wet season (Trott & Alongi, 1999). Chlorophyll *a* concentrations in the Klang mangrove, Malaysia, increase following tidal or freshwater flushing (Thong et al., 1993). However, phytoplankton blooms may not only immediately respond to nutrient input but also only after a lag period during which the nutrient concentration gradually builds up. This is the case in the MMFR where heavy rainfall and subsequent salinity depression were observed in the month prior to the peak concentration of chlorophyll *a* in January 2003 (see Fig. 3). The peak recruitment (November 2002) of copepods in MMFR waterways seemed to occur prior to the phytoplankton bloom in January 2003, and can be explained as a reproductive strategy adopted by copepods in order that newly recruited young are timed to exploit the larger biomass of phytoplankton (see Fig. 3).

Notwithstanding the importance of phytoplankton carbon to zooplankton, the contribution of micro-phytobenthos may be significant in the lower estuary and shallow nearshore waters as shown by stable isotope studies (Newell et al., 1995; Chong et al., 2001; Chew et al., 2007).

Copepod as potential food in mangrove and nearshore waters

The MMFR waterways and adjacent mudflat are populated by juveniles of commercially important fish and shrimps (Chong, 2005). Our results showed that copepods are numerically abundant in MMFR waterways and nearshore waters. Considering that copepods are the major food items in pelagic food webs, their abundance in the estuary will have considerable impact on the trophodynamics of the mangrove ecosystem. Chew et al. (2007) reported that more than 50% of the examined 2,123 juvenile and small fish that belonged to 26 species in MMFR waterways fed on copepods. Predominant mangrove and mudflat fish species, such as ambassids, ariids, and engraulids (Sasekumar et al., 1994) consumed copepods that together comprised >50% of their stomach contents (Chew et al., 2007). Post-flexion engraulid larvae were reported to be very abundant at the time when copepods were also found to be abundant in the MMFR waterways (Ooi et al., 2005, 2007). *Pseudodiaptomus*, *Acartia*, *Parvocalanus*, and *Oithona* were the main copepods consumed by zooplanktivorous fish in MMFR (Chew et al., 2007).

Conclusion

The abundance and community structure of copepods in the Matang estuary and adjacent coastal waters showed that spatio-temporal variations related to the physical and chemical parameters that varied with the prevailing rainfall pattern. Copepod abundance and chlorophyll *a* concentrations were higher in mangrove and nearshore waters than in offshore waters. Both copepod and phytoplankton abundance peaked during the NE monsoon when rainfall was highest. The copepods in Matang waterways and adjacent coastal waters were dominated by *Acartia*, *Parvocalanus*, and *Oithona* spp. Salinity and chlorophyll *a*

concentrations appear to be the two major controlling factors of copepod diversity in the estuary.

Acknowledgments We thank JIRCAS and University of Malaya (UM) for funding this project, and UM for providing research facilities. We express our gratitude to the Fisheries Department, Malaysia for their cooperation, and provision of trawling permit. We are grateful to S. Nishida, B. H. R. Othman, C. Walter, and T. Yoshida for their assistance on copepod species identification. Special thanks to the following persons for field and laboratory assistance: Mr. Lee Chee Heng (boat man), Miss Ooi Ai Lin, Dr. A. Sasekumar, and members of the Mangrove Ecology Group, University of Malaya. This study forms part of a Ph.D. thesis undertaken by the first author.

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